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ISSN 0038-3872

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 109 **Number 1**

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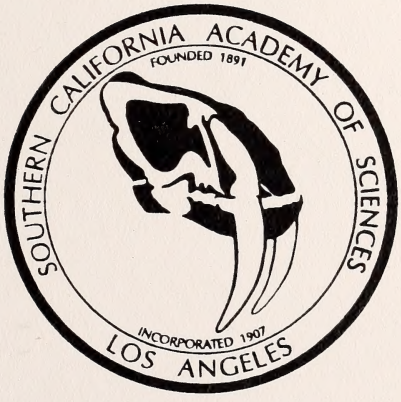

BCAS-A109(1) 1–21 (2010) **April 2010**

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Date of this issue 6 May 2010

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109(1), 2010, pp. 1–7
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Avian material from Rancho del Oro, a Pleistocene locality in San Diego County, California

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Abstract.—Late Pleistocene avifaunal material from a construction site in Oceanside, California is described. The material includes 77 bones from 21 species, only one of which (*Podiceps parvus*) is extinct. Two previously described Pleistocene species (*Oxyura bessomi* and *Bucephala fossilis*) are placed in extant species. The first fossil record for *Phalaropus lobatus* is recorded.

In 1994 a lacustrine sandstone containing vertebrate material was discovered at a construction site in Oceanside, California (33° 4′26″N, 117° 7′25″W). Approximately 500 kg of matrix were removed and dry screened through 1/8 in mesh. The site was subsequently graded away. The locality, named Rancho del Oro, has yielded bones of turtle, anuran and fish (*Mugil* sp.) as well as twenty-one avian taxa, now cataloged at the San Diego Natural History Museum (SDNHM). Table 1 presents a list of these taxa and comments on each species appear below.

Table 1. Avian species from Rancho del Oro, late Pleistocene of Oceanside, California.

Taxa	No. bones
Aechmophorus occidentalis/clarki	3
Podilymbus podiceps	11
Podiceps parvus	4
Pelecanus, cf. *P. erythrorhynchus*	1
Anas clypeata	1
Aythya affinis	3
Bucephala albeola fossilis	3
Oxyura jamaicensis	16
Anatid	4
Calipepla californica	3
Rallus limicola	2
Fulica americana	11
Phalaropus lobatus	1
Geococcyx californianus	2
Apheloocoma californica	1
Vireo sp.	1
Toxostoma redivivum	5
Piranga ludoviciana	1
Melospiza cf. *M. melodia*	1
Emberizid sp.	1
Agelaius phoeniceuus	2
total number of bones	77

Aechmophorus occidentalis (Lawrence) or ***A. clarkii*** (Lawrence)

Material: SDNHM 50700, partial skull; 45102, left distal coracoid; 50679 phalange.

The San Diego bones are inseparable from those of the two living species of *Aechmophorus*, which cannot be separated on the basis preserved material.

The only other named species of Pleistocene *Aechmophorus* is *A. lucasi* from Fossil Lake, Oregon (Miller 1911), which was subsequently shown to be inseparable from recent material of *A. occidentalis* (Storer 1989). Storer also noted that "no valid differences between skeletal elements of the two species (*A. occidentalis* and *A. clarkii*) have been found yet" (Storer 1989:322).

Podilymbus podiceps (Linnaeus)

Material: SDNMH; 50668, distal right humerus; 51597 and 51598, distal left humeri; 51604 and 51605, right coracoids; 50673 and 61249, distal right ulnae; 50601, proximal left unla; 50699, proximal right tibiotarsus; 51612, right tarsometatarsus; 50697 vertebra.

Two specimens, 51598 and 50601, are slightly more robust than modern material of this species. Howard (1946) noted the large size difference between males and females of living members of this species, a difference which led Shufeldt (1913) to mistakenly name some specimens from Fossil Lake as a new species *P. magnus*.

Podiceps parvus (Shufeldt)

Material: SDNHM 50661, right ulna; 50692, right scapula; 50693-94, left carpometacarpus; 51621, tip of premaxilla.

Shufeldt (1913) based *Podiceps parvus* on material from Fossil Lake Oregon. The bones were intermediate in size between *Aechmophorus* and the smaller *P. nigricollis* and *P. auritus*, being slightly smaller than *P. grisegena* with which it shares this intermediate size (Howard, 1946). Howard (1949a) referred Pliocene material from San Diego to this species. Later, in reviewing the Pleistocene material from Vallecito Creek deposits in the Anza Borrego Desert, she noted (1963) that while other bones agreed in size with *P. parvus*, the tarsometatarsi from Vallecito are longer than the type material of *P. parvus* and are larger than *P. grisegena*.. Howard, therefore, considered both the Pliocene and Pleistocene material from San Diego as a different, longer-legged species which she listed as *Podiceps* sp. in her 1963 paper. The current material from Rancho del Oro agrees in size with the type collection of *P. parvus*. The ulna (50693-4) has a maximum length of 91.15 mm. Although the ulna assigned to this species from Fossil Lake was unmeasurable, this measurement agrees with other measurements of *P. parvus* as being slightly smaller than specimens of living *P. grisegena*. The carpometacarpus has a maximum length of 40.65 mm, which is smaller than material referred here from Fossil Lake, Oregon but may reflect sexual dimorphism in grebes. The premaxilla seems slightly smaller but similar in configuration to that of *P. grisegena* and quite unlike the bills of other grebes. I know of no living grebe whose body proportions could be considered especially long-legged, and believe it just as likely that there are two grebes represented in the Vallecito Creek material rather than a single grebe with longer legs. Be that as it may, it is impossible to separate the Rancho del Oro material from the type material of *P. parvus*.

Pelicanus erythrorhynchus Gmelin

Material, SDNHM 51624, fragments of a synsacrum

These fragments, including a partial articular surface with the vertebral column, are more the size of this species than *P. occidentalis*.

Anas clypeata Linnaeus

Material: SDNHM 50696, distal left coracoid

This bone is inseparable from recent material of this species.

Aythya affinis (Eyton)

Material: SDNHM 50665, proximal left ulna; 51603, right coracoid; 51619, a partial synsacrum.

These bones are nearly identical to recent material of this species. On the ulna, the scar of the anterior articulate ligament and ridges around the impression of the brachialis anticus are much more similar to *Aythya* than to species of *Anas*. The coracoid is slightly small for *A. affinis*, but closer in size to this species than to *A. americana* or *A. marila*. The ridge along the edge of the triosseal canal is quite unlike the pattern seen in *A. collaris*.

Bucephala albeola fossilis (Howard) new combination

Material: SDNHM 50687, right proximal ulna; 50689, right proximal carpometacarpus; 50695, phalange.

Three bones of a small duck are referable here rather than to teal or ruddy duck. Howard (1963) named a new species, *Bucephala fossilis*, based on material in the Vallecito Creek fauna. Her diagnosis indicated most bones were similar in size to *B. albeola*. Her distinguishing characteristics on the type bone, a carpometacarpus, were based on the shape of the process of metacarpal I, which is missing from SDNHM 50689. She noted some slight size differences in ulna between her species and recent material. The San Diego material agrees with the type material of B. *fossilis* in that the ulna is identical in size to recent material of *B. albeola*, but the carpometacarpus is longer. Measurements of the carpometacarpus of the type, compared to recent material and SDNHM 50689 are as follows

Measurements in mm of carpometacarpus	Type of B. *fossilis*	SDNHM 50689	*Bucephala albeola*			
			n.	min	max	mean
max. width of prox. end anterior to ext. ligamental attachment	4.15	3.93	6	3.40	4.32	4.01
prox. end to distal edge of process for metacarpal I	8.58	8.62	6	7.52	8.44	7.93

The living species *Bucephala albeola* has been described from Pleistocene deposits at Fossil Lake, Oregon (Shufeldt 1913), McKittrick (Miller 1935) and San Pedro (Howard 1949b), as well as deposits in Kansas, Virgina and Florida (Brodkorb 1964b). As there is overlap in nearly all characteristics between *B. albeola* and *B. fossilis*, I consider *B. fossilis* as distinct only as the subspecific level.

Oxyura jamaicensis **(Gmelin)**

Material: SDNHM 50664, right distal humerus; 51595, fragmentary left humerus; 50660, left humerus; 50686 right humerus; 51600 left ulna; 50667, proximal right ulna; 50674, distal right ulna; 51608, left carpometacarpus; 51606, left coracoid; 51611, left scapula; 50666 distal left tarsometatarsus; 50669, synsacrum; 50680, claw; 51623, 3 phalanges

As might be expected from a fresh water pond, *Oxyura* is one of the commonest species present. Bones referred here are nearly identical to *O. jamaicensis* in configuration, but are slightly smaller (Table 2). They are quite unlike *O. dominica*, both in size and morphology.

Table 2. Measurements of *Oxyura jamaicensis*.

	San Diego				Recent			
	N	min	max	mean	N	min	max	mean
Humerus; max length	2	65.38	67.97	66.67	8	66.12	71.80	69.33
Humerus;max distal width	3	8.26	8.64	8.51	7	8.38	9.14	8.84
Ulna; max length				54.34	8	57.12	62.42	60.65
Carpometacarpus; max length				32.03	8	33.65	35.83	34.92
coracoid, max length				36.46	8	36.59	39.50	38.33

The living species of ruddy duck, *Oxyura jamaicensis*, has been identified from late Pleistocene deposits at Fossil Lake (Howard 1964) and Lake Manix (Jefferson 1985). The only other Pleistocene species of *Oxyura* is *O. bessomi*, described by Howard (1963) from Vallecito Creek. This species was based on a nearly complete carpometacarpus and referred ulna and coracoids. Howard considered the type carpometacarpal bone to be quite odd, and was "tempted to assign this fossil species to a distinct genus" (Howard 1963:14). I find this type carpometacarpus unlike *Oxyura* in at least four characteristics:

1. the proximal end between the carpal trochlea is flat, not notched as in *Oxyura*,
2. the process of metacarpal I is more upright, especially on its distal surface, not slanted as in *Oxyura*.
3. the internal ligamental fossa is fairly deep, not shallow as in *Oxyura*, and.
4. the internal carpal trochlea is anteriorly rounded, not somewhat pointed as in *Oxyura*.

The maximal height of the proximal end of the carpometacarpal in the type of *O. bessomi* is 8.22 mm, which compares to an average height (n=8) of 8.30 in *Anas crecca* and 7.43 mm and 7.84 mm in female and male *Oxyura jamaicensis*. In the features listed above, the type specimen of *O. bessomi* is similar to *Anas crecca*. The slightly larger size of the type of *O. bessomi* (length of the carpometacarpal from the proximal end to the tip of the facet for digit III is 33.51 mm in the type specimen and 35.11 mm in female and 37.33 mm in male *Anas crecca*) may warrant retention as a separate species within the genus *Anas*. The remaining bones from Vallecito Creek seem correctly assigned to *Oxyura* and, like the material listed here, are slightly smaller than recent material of *O. jamaicensis*. This size difference is not enough, in my opinion, to warrant separate specific status, leaving *O. jamaicensis* as the only Pleistocene species of *Oxyura*.

Anatidae

Material SDNHM 50676, phalange; 50698, 50675, 51620, vertebrae

All material is from a medium sized duck but cannot be accurately assigned to species.

***Callipepla californica* (Shaw)**

Material: SDNHM 50662 proximal humerus; 50691, a coracoid; 51610, fragmentary carpometacarpus.

The referral of this material to *Callipepla californica* and not C. *gambelii* is based soley on the current range of the two species.

Rallus limicola Vieillot

Material: SDNHM 50690, a distal tibiotarsus; 50670 proximal tarsometatarsus.

These bones are inseparable from the living species.

Fulica americana Gmelin

Material: SDNHM 51599, left distal humerus; 50672, right distal ulna; 51602, left distal radius; 51609, right distal carpometacarpus; 51607, left coracoid; 50681, left scapula; 51622, sternal fragment; 51625, right distal tibiotarsus; 50677, phalange; 50678, phalange; 51623, 5 phalanges.

Fulica americana is the only valid species of this genus known from the Pleistocene of the continental United States. The Rancho del Oro material is identical to living coots, except that the ulna and tibiotarsus are slightly more slender.

Pleistocene coots from Fossil Lake, Oregon were described as a new species, *F. minor*, by Shufeldt (1892). Howard (1946), with more material, showed that although slightly different in mean size, most of the Fossil Lake material fell within the size range of living coots and, on that basis, relegated Shufeldt's species to subspecific status under *F. americana*. (Although Whetmore (1956) resurrected the name *F. minor*, Brodkorb (1964a) renamed this species *F. shufeldi* as the name *F. minor* was preoccupied.)

Howard (1946) noted that the Fossil Lake material had slightly longer leg bones and slightly shorter wing bones than recent material, and (1967) designated Fossil Lake specimens as *F. a. shufeldi*.

Howard (1963) described *Fulica hesterna* based on material from the Vallecito Creek Olson (1974) in a review of Pleistocene rails, considered this species to be a synonym of *F. americana*, despite its slightly larger size. He noted that several Pleistocene precursors of modern species, including *F. americana* and *Rallus limicola*, were slightly larger and attributed this to cooler climates during Pleistocene glaciation.

Phalaropus lobatus (Linnaeus)

Material: SDNHM 51627, a left carpometacarpal

This bone is identical to material of the living species. Rubega et al. (2000), quoting Olsen (1985) states that there is no fossil record of this species.

Geococcyx californicus (Lesson)

Material, SDNHM 51617, a proximal right tibiotarsus; 51623, first phalange of second digit.

These bones are at the small end of the size range for the living species but assignable here.

Passeriformes

The bones of many species of passerines are nearly identical. The identifications here are based on comparisons with the most common species from wet riparian and coastal sage habitats in southern California.

Aphelocoma californica (Vigors)

Material: SDNHM 50671, a right distal femur.

This femur is slightly less robust than that in the living species, but is best referred here.

***Vireo* sp.**

Material: SDMNH 50684, left proximal coracoid

This small bone seems assignable to the Vireonidae, and is about the size of warbling vireo, *V. gilvus*.

Toxostoma redivivum (Gambel)

Material: SDMNH 51626, proximal left humerus: 51614 and 51615, distal right tarsometatarsi; 51616, distal left tarsometatarsus; 51613, proximal right tarsometatarsus;

These bones are inseparable from material of the living species.

Piranga ludoviciana (Wilson)

Material: SDMNH 51628, a distal right coracoid.

This coracoid is identical to modern material of this species.

Melospiza* sp. cf. *M. melodia (Wilson)

Material: SDNHM 50659, right humerus

This bone is identical to living *Melospiza melodia*, but cannot be definitely assigned due to similar humeri of several other sparrow taxa.

Emberizidae

Material: SDNMH 50683, a distal left coracoid.

This bone is similar in size and configuration to material of *Melospiza lincolnii*, but I could not compare it to all possible species of erberizids.

Agelaius phoeniceus (Linnaeus)

Material: SDNHM 51596, a proximal left humerus; 51618, a distal right tibiotarsus;.

These bones are inseparable from those in the living species.

Discussion

Based on the identified fauna, the Rancho del Oro assemblage is considered late Pleistocene in age. Comparable deposits of similar age are the mid-Pleistocene fluvial deposits at Vallecito Creek in the Anza-Borrego Desert of eastern San Diego County (Howard 1963; Jefferson 2006), material from late Pleistocene Fossil Lake Oregon (Miller 1911; Howard 1946; Jehl 1976), the late Pleistocene Rancho La Brea fauna from Los Angeles (Howard 1962) and the lacustrine material from late Pleistocene Lake Mannix (Howard 1955; Jefferson 1985) in the Mojave Desert of San Bernardino County. The Rancho del Oro assemplage, however, lacks the raptoral birds associated with tar seeps (Rancho la Brea) and species (eg. flamingos) associated with inland desert lakes like Fossil Lake and Lake Manix.

Except for *Podiceps parvus*, all material is assigned to extant lineages, although in some cases differing at the subspecific level. The avian species present are what one would expect at a fresh water lagoon along the California coast, with a surrounding vegetation of coastal sage scrub.

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Bull. Southern California Acad. Sci.
109(1), 2010, pp. 8–14
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Morphological and Anatomical Characteristics of Blackbrush (*Coleogyne ramosissima* Torr.) Leaves: A Review of Literature

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Abstract.—Leaves of blackbrush (*Coleogyne ramosissima* Torr.) shrubs share a number characteristics of leaves of both xerophytic and sclerophyllous shrubs. Despite some leaf surface (morphological) and anatomical similarities with typical xerophytic leaves, blackbrush leaves are more similar to typical semi-arid coastal chaparral plants in Mediterranean and southern California, or cool and high elevation inland desert perennial plants. Semi-deciduous, thick blades, well-cutinized epidermises, numerous small leaves, sclerophyllic leaves, hypostomatry, sunken stomata, thickened epidermal cell walls, and abundant abaxial and adaxial trichomes are characteristics of blackbrush plants, as well as typical woody xerophytic and sclerophyllous plants. Blackbrush also exhibit summer dormancy, with characteristics of revolute margins, uniseriate hypodermis, biseriate epidermis, bifacial palisade parenchyma, and intercellular air space in leaves; all of which are characteristics of leaves from sclerophyllous chaparral plants. Overall, xerophytic and sclerophyllous leaf designs are similar among blackbrush, warm desert plants, and semi-arid coastal chaparral plants, presumably due to many climatic and edaphic attributes shared by the inland Mojave Desert and coastal southern California. Because of a lack of consensus in current literature, morphological and anatomical characteristics of blackbrush leaves continue to be a curious dilemma to many botanists and plant ecologists.

Introduction

Blackbrush (*Coleogyne ramosissima* Torr.) is a shrub occurring at mid-elevations in the Mojave Desert. Blackbrush occur primarily along the Colorado River drainage and several adjacent enclosed basins of the Great Basin-Mojave Desert transition zone (Bowns and West 1976, Pendleton and Meyer 2004). Blackbrush leaves share some of the characteristics of xerophytic leaves that are typically small with reduced cell size, thick cuticle and blades, cylindrical, well-developed palisade mesophyll, and dense adaxial pubescence (Rundel and Gibson 1996). Such leaf design is generally interpreted as a response to arid habitats with water deficits and poor soil nutrients (Beadle 1966, Rundel and Gibson 1996). Blackbrush leaf anatomy shows features of typical of many desert species (Bowns 1973, Bowns and West 1976). However, recent morphological and anatomical investigations have revealed that blackbrush leaves do not possess typical internal xerophytic leaf design (Gibson 1996, Rundel and Gibson 1996) despite their xeromorphic appearance. Plants, having revolute leaf margins and hypostomatic leaves with hypodermis, are common in some sclerophyllous scrub (Coastal chaparral) communities of Mediterranean-type climate in southern California or cool and high elevation (semi-arid) xerophytic plant communities in warm deserts (Gibson 1996).

Table 1. A comparison among leaf morphology of blackbrush, typical woody xerophytic, and typical sclerophyllous Mediterranean (coastal) chaparral plants. The letter "X" indicates the presence of a leaf characteristic (Gibson 1996). A parenthesis around an "X" also indicates a characteristic of xerophytic or sclerophyllous plants based on the study of (Lei 1999).

Morphological traits	Blackbrush	Xerophyte	Sclerophyll
Summer dormancy	X		X
Numerous leaves	X	(X)	(X)
Evergreen or semi-evergreen	X		X
Thick blade	X	(X)	(X)
Small-sized leaves	X	(X)	(X)
Tough, leathery (rigid) leaves	X	(X)	X
Revolute leaf margin	X		X
Adaxial trichomes	X	X	X
Abaxial trichomes	X	X	X
Amphistomatry		X	X
Hypostomatry	X	(X)	X
Sunken stomata	X	(X)	X

Although the Mojave climate is an arid continental desert, it resembles Mediterranean climate with cool winters, light precipitation and warm, dry summers (Rowlands et al. 1977). The North American monsoons cause episodic thundershowers from July through September annually.

Previous research studies by Bowns (1973), Bowns and West (1976), Gibson (1996), Rundel and Gibson (1996), and Lei (1999) have increased our understanding regarding the anatomical features of blackbrush leaves. The former two research studies found that blackbrush leaf anatomy show features typical of xerophytic shrubs. In contrast, the latter three studies found that blackbrush anatomy is more typical of semi-arid coastal (Mediterranean) chaparral than arid inland desert shrubs. The current literature apparently does not agree whether blackbrush is a xerophytes or a sclerophyll. This article reviews blackbrush leaf surface (morphological) and anatomical features, and attempts to determine whether such features are more similar to xerophytic or to sclerophyllous leaves based on the data collected from previously published literature.

Morphological Characteristics

Blackbrush and chaparral plants have adapted to a summer drought and winter rain climatic pattern. Blackbrush are semi-evergreen, often experiencing summer dormancy to the extent that portions of their leaves desiccate and fall off during dry summer seasons. This phenomenon is shared by most chaparral plant species (Bakker 1984). In summer months, leaves of blackbrush and many chaparral plants are semi-evergreen, which also occurs in some xerophytic plants in order to conserve water. Summer months are typically the time of dormancy. In general, the most active growth season is from late winter through spring when soil moisture and air temperatures are optimal for growth conditions (Bakker 1984).

Leaves of blackbrush contain abundant trichomes (Table 1), especially on the abaxial surface. Dense pubescens is effective in blocking excess sunlight and in reducing water loss (Rundel and Gibson 1996). Small, thick leathery leaves of blackbrush and typical chaparral plants can greatly reduce moisture loss and are well-adapted to xeric sites. A strong correlation exists between leaf size and habitat aridity, with more xeric sites tend to support shrubs with smaller leaves (Bakker 1984).

Table 2. A comparison among leaf anatomy of blackbrush, typical woody xerophytic, and typical sclerophyllous Mediterranean (coastal) chaparral plants. The letter "X" indicates the presence of a leaf characteristic (Gibson 1996). A parenthesis around an "X" also indicates a characteristic of xerophytic or sclerophyllous plants based on the study of (Lei 1999).

Anatomical traits	Blackbrush	Xerophyte	Sclerophyll
Reduced cell size	X	(X)	(X)
Well-cutinized epidermises	X	X	X
Thickened epidermal cell wall	X	(X)	X
Uniseriate epidermis		X	
Biseriate epidermis	X		X
Hypodermis	X		X
Bifacial palisade	X		X
Isolateral palisade		X	
Intercellular air space	X		X

Blackbrush leaves exhibit sunken stomata that are evident early in leaf development, but become more prominent as the leaf matures (Bowns 1973, Bowns and West 1976). Blackbrush leaves are hypostomatic (Table 1), implying that stomates are located on the abaxial epidermis only. Stomates are connected to large substomatal chambers (Bowns 1973). Gibson (1996) state that more than 90% of non-succulent woody species in warm, inland deserts have amphistomatic leaves. However, hypostomatry has been observed in blackbrush shrubs, which are most common in semi-arid upland sites (Gibson 1996). Plants with hypostomatic desert leaves are probably not successful colonizers of warm desert habitats (Gibson 1996).

Anatomical Characteristics

Blackbrush leaves contain a double-layered (biseriate) epidermis (Table 2) that is small, dense, and flat. Blackbrush leaves have thick, well-developed waxy cuticle on leaf blades and thick epidermal cell walls (Table 2). The cuticle is thick in proportion to the leaf size, and is especially thick near the point of attachment of the epidermal hairs (Bowns 1973, Bowns and West 1976). Immediately beneath the biseriate epidermal cells, a relatively thick, highly vacuolated layer of uniseriate hypodermis is observed (Table 2). Hypodermis, having either collenchymas or sclerified cell walls, appears in blackbrush from relatively cool habitats, and is atypical of non-succulent warm desert plants (Gibson 1996). Although the precise function of hypodermis is not well understood, perhaps it is a mechanism to reduce transpiration and/or to resist tissue damage due to wilting and strong wind (Gibson 1996). A hypodermis occurs more often in tough sclerophyllous leaves; thinner, softer leaves generally do not have a hypodermis (Mauseth 1988). Bowns (1973) proposes that blackbrush leaf is made rigid and is supported by hypodermis (sub-epidermal collenchymas), which is especially well-developed near the adaxial surface. The presence of dense, uniseriate hypodermis may be largely contributed to the toughness and rigidity of blackbrush leaves, which in turn may endure extensive summer drought periods.

Below the hypodermis, the palisade parenchyma is readily distinguished from the spongy parenchyma (Table 2). The palisade parenchyma consists of multiple elongated (column-like) cells, mainly in the direction perpendicular to the leaf surface. Blackbrush leaves are bifacial. Palisade parenchyma of two- to three-layers thick (deep) occurs on the adaxial side only, and is filled with abundant chloroplasts. Gibson (1996) states that

Table 3. Geographic characteristics of southern Nevada blackbrush, southern California coastal chaparral, and warm, inland Mojave Desert Shrublands (From Horton and Kravel 1955, Hanes 1971, Barbour et al. 1987, and Gabler et al. 2005). An approximation of elevation, latitudinal, and longitudinal ranges is shown below.

Geographic Variables	Blackbrush	Mojave Desert	Chaparral
Elevational range (m)	1,160 to 1,830	Below 1,525	Below 1,830
Latitudinal range (N)	35°04′ to 41°15′	33°10′ to 38°21′	32°05′ to 35°06′
Longitudinal range (W)	114°01′ to 118°55′	113°30′ to 117°04′	116°17′ to 124°44′
Geographic zone	Inland	Inland	Coastal

typical desert leaves possess isolateral mesophyll, having at least some palisade parenchyma on the abaxial side or many palisade parenchyma layers throughout the transaction and frequently continuing around leaf margins. Multiple layers of palisade parenchyma occur in plants exposed to strong sunlight and the lower layers would receive enough light to photosynthesize effectively (Mauseth 1988).

The spongy parenchyma of blackbrush leaves is considerably less dense compared to palisade parenchyma, and contain rounded cells immediately beneath the palisade parenchyma, intermixed with some intercellular air space on the abaxial side of the blade (Lei 1999). Conversely, Mauseth (1988) states that in typical xerophytic plants, the spongy mesophyll may be lost altogether with only palisade parenchyma remaining, or there may be no intercellular spaces at all (Mauseth 1988). Such arrangement greatly reduces the ability to absorb carbon dioxide, but the benefit of water conservation apparently offsets this phenomenon (Mauseth 1988).

Relatively few shrubs species in warm, inland desert tend to have hypodermis, sunken stomata, and thickened epidermal cell walls (Gibson 1996). However, this statement is highly debatable because sunken stomata and thickened epidermal cells are also common adaptations in warm, inland desert plants. The sclerophyllous leaf design reveals an affinity of some southern Nevada plant species' morphology and anatomy with semi-arid coastal chaparral species as opposed to typical arid inland xerophytic plants, although sclerophyllous and xerophytic leaves share a number of common characteristics.

Plants from the Rosaceae family, including blackbrush generally do not occur in the most arid (dry) desert sites (Gibson 1996). Yet, the Rosaceae family is well represented in the cold desert of the Great Basin and in the chaparral vegetation of southern California (Mooney and Dunn 1970). In the southwestern United States, blackbrush shrubs occur in the transition zone between the cold desert and warm desert (Pendleton and Meyer 2004). Nevertheless, blackbrush shrubs do not occur in low Mojavean valleys of southern Nevada. The absence of blackbrush in the low Mojavean valleys is not strictly a function of elevation per se; perhaps many environmental attributes are associated with changing elevation.

Climatic and Geographic Attributes

Inland Mojave Desert shrublands and coastal Mediterranean chaparral shrublands share a number of geographic and climatic attributes in common (Tables 3 and 4, respectively). For instance, semi-arid Mediterranean climatic regions are found between 30 and 45 degrees north and south latitudes, on the west coasts of major continents, and in the Mediterranean Sea region (Barbour et al. 1987). Southern Nevada and southern California apparently lie within this latitudinal belt (Table 4). Both xerophytic and

Table 4. Climatic attributes of southern Nevada blackbrush, southern California chaparral, and warm Mojave Desert shrublands (From Horton and Kravel 1955, Hanes 1971, Bowns and West 1976, Barbour et al. 1987, Gabler et al. 2005, as well as Lei and Walker 1997).

Climatic variables	Blackbrush	Mojave Dessert	Chaparral
Air temperature			
Summer	Very high	Very high	High
Winter	Low	Mild	Low
Precipitation			
Summer	Very low	Very low	Very low
Winter	Low	Very low	Low
Sunny days	Many	Many	Many
Cloud cover	Very little	Very little	Little
Fog	Rare	Rare	Moderate
Relative humidity	Very low	Very low	Mild
Evaporation	Very high	Very high	Mild
Evapotranspiration	High	High	Moderate

sclerophyllous plants must endure prolonged summer droughts regardless of the amount and timing of winter precipitation (Miller et al., 1983). The arid continental desert of southern Nevada resembles the coastal Mediterranean-type climate characterized by cool winters with light precipitation and warm, dry summers in addition to long periods of sunny days and cloudless skies (Barbour et al. 1987, Munz 1974). The Mediterranean-type climate has more precipitation concentrated in cool winter months and summer drought annually, along with warm to hot summer and mild winter air temperatures (Table 4). In southern Nevada and California, rarely more than one inches of rainfalls occur during summer months (Specht 1968), with an exception of occasional major storm events. Typically, summer thunderstorms are episodic, short in duration, and may be so intense locally that most water will run off the soil surface before water infiltration process occurs (Barbour et al., 1987). Southern California has a year-round, marine-moderated atmosphere with coastal fogs, which are more frequent in spring and summer than in autumn and winter seasons (Hanes 1971). Nevertheless, southern Nevada is an arid continental desert due to the present of the Sierra Nevada in California intercepting moisture-laden Pacific winds, thus forming rainshadows and resulting in arid climate with warm desert landscapes.

Edaphic Attributes

Both inland Mojave Desert and coastal chaparral shrublands also share a number of edaphic attributes in common (Table 5). For instance, xerophytic and sclerophyllous plants often occur on gravelly/stony soils with little organic matter (Table 5, Barbour et al. 1987). Desert and chaparral soils generally have low water content and available nutrients (Table 5), including deficiencies in nitrogen, phosphorus, potassium, and sulfur (Specht 1968). By enduring the unfavorable and imbalanced chemical ratio of soil, extensive monospecific blackbrush and chaparral shrublands benefit from the near absence of competing woody perennial plants (Bakker 1984). Low soil moisture is largely associated with low annual precipitation. Desert and chaparral soils are relatively shallow with no distinct soil profiles (Table 5) due to the presence of hardpan (Specht 1968). Blackbrush shrublands containing dense monospecific blackbrush stands are frequently found at mid-elevations with relatively cool, semi-arid habitats in southern Nevada. The

Table 5. Edaphic attributes of southern Nevada blackbrush, southern California chaparral, and warm Mojave Desert shrublands (From Specht 1968, Hanes 1971, Bowns and West 1976, Barbour et al. 1987, Gabler et al. 2005, as well as Lei and Walker 1997).

Edaphic variables	Blackbrush	Mojave Dessert	Chaparral
pH	Slightly alkaline	Moderately alkaline	Slightly acidic
Moisture	Low	Very low	Low
Depth	Very shallow	Very shallow	Shallow
Organic content	Low	Very low	Low
Mineral nutrient	Very low	Very low	Very low
Surface	Stony/gravelly	Stony/gravelly	Stony/gravelly
Texture	Sandy	Sandy	Sandy-loam
Parent material	Limestone/domolite	Limestone/domolite	Igneous/metamorphic
Profile	Not distinct	Not distinct	Not distinct

sclerophyllous leaf design in blackbrush may also be associated with, or an adaptation to, arid habitats with infertile edaphic conditions and water deficiencies during arid summer seasons (Beadle 1966).

Conclusions

No consensus from currently literature has been reached to determine whether blackbrush is a xerophytes or a sclerophyll since blackbrush leaves possess a number of morphological and anatomical traits that are common in both woody xerophytes and sclerophylls. Such traits include semi-evergreen, thick blades and cuticle, abundant small leaves, tough leathery (rigid) leaves, hypostomatry, sunken stomata, thickened epidermal cell wall, as well as dense abaxial and adaxial pubescens. Additionally, blackbrush shrubs often exhibit summer dormancy, with characteristics of revolute margins, uniseriate hypodermis, biseriate epidermis, bifacial palisade parenchyma, and intercellular air spaces in leaves, which are sclerophyllous traits in leaves of chaparral plants.

The precise distinctions between xerophytes and sclerophylls are not conspicuous, presumably due to many similar environmental attributes between semi-arid coastal sclerophyllous chaparral and arid continental Mojave Desert shrublands. Nonetheless, this review article suggests that blackbrush are more similar to coastal chaparral plants in southern California than to low-elevation inland desert plants in southern Nevada from morphological and anatomical perspectives.

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Bull. Southern California Acad. Sci.
109(1), 2010, pp. 15–17
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Research Note

Reproduction in Cope's Leopard Lizard, *Gambelia copeii* (Squamata: Crotaphytidae)

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Gambelia copeii is endemic to Baja California, Mexico, and ranges from extreme southern San Diego County, California, south to Todos Santos on the west coast of the Cape Region, Baja California (Grismer 2002, Mahrdt et al. 2010). Information on its reproduction is limited to brief accounts (Fitch 1970, McGuire 1996, Grismer 2002, Stebbins 2003, Lemm 2006, Mahrdt and Beaman 2009). The purpose of this paper is to provide more information on the reproductive biology of *G. copeii* from a histological examination of museum specimens as part of an ongoing analysis of the reproductive patterns of reptiles from Baja California (e.g., Goldberg and Beaman 2003, 2004). The use of museum specimens in life-history studies is becoming increasingly valuable as it is often impossible to collect lizards from native populations. Elucidation of the reproductive strategy is fundamental in documenting the life history of a species and is important in the formulation of conservation policies.

We examined a sample of 39 *G. copeii* consisting of 16 males (mean snout-vent length, SVL = 94.8 mm ± 8.2 SD, range: 80–108 mm) and 23 females (mean SVL = 103.5 mm ± 11.1 SD, range: 83–133 mm) from San Diego County, California, and Baja California, Mexico from the California Academy of Sciences (CAS), Natural History Museum of Los Angeles County (LACM), Museum of Vertebrate Zoology (MVZ), and San Diego Society of Natural History (SDSNH) (Appendix I). Lizards were collected 1922–1978.

The left testis was removed from males and the left ovary was removed from females for histological examination (Presnell and Schreibman 1997). Enlarged follicles (> 5 mm) and/or oviductal eggs were counted. Tissues were embedded in paraffin, sectioned at 5μm, and stained with hematoxylin followed by eosin counterstain. Ovary slides were examined for yolk deposition or corpora lutea. Testes slides were examined to ascertain the stage of the testicular cycle present. Mean body sizes of male versus female *G. copeii* were compared using an unpaired *t*-test and the relationship between body size (SVL) and clutch size was examined by linear regression. Statistical tests were performed using Instat (vers. 3.0b, Graphpad Software, San Diego, CA).

Monthly stages in the testicular cycle of *G. copeii* are shown in Table 1. Two stages were present in our samples: (1) spermiogenesis (sperm formation), in which the seminiferous tubules are lined by clusters of mature spermatozoa and/or metamorphosing spermatids; and (2) regressed, in which sperm production has ceased, seminiferous tubules are reduced in size, and the dominant cells present are spermatogonia and Sertoli

Table 1. Monthly changes in the testicular cycle of *Gambelia copeii*.

Month	n	Regression	Spermiogenesis
March	1	0	1
April	4	0	4
May	2	0	2
May–June	1	0	1
June	7	0	7
August	1	1	0

cells. *Gambelia copeii* appears to follow a testicular cycle typical of other lizards from the North American temperate zone characterized by a spring-summer period of spermiogenesis followed by late summer regression (e.g., Goldberg 1974, 1975). One male from June was in a late stage of spermiogenesis in which the germinal epithelium was reduced to 5–6 layers, although sperm were still being produced. Spermiogenesis was almost complete in this male. The smallest reproductively active males in spermiogenesis were captured in June and measured 80 mm SVL (SDSNH 5078, 5079).

The mean female body size of *G. copeii* significantly exceeded that of males (unpaired *t* test, $t = 2.66$, $df = 37$, $P = 0.0114$). Monthly stages in the ovarian cycle of *G. copeii* are shown in Table 2. Five stages were present in the ovarian cycle: (1) no yolk deposition (quiescent); (2) early yolk deposition with basophilic yolk granules present; (3) enlarged preovulatory follicles (> 5 mm diameter); (4) oviductal eggs with eggs in oviducts; and (5) corpora lutea, indicating an egg clutch had been deposited. Because of museum policy, clutch sizes (consisting of enlarged follicles > 5 mm) from specimens SDSNH 18946 (June) and SDSNH 26752 (March) were not counted. The oviductal eggs in CAS 56105 (July) were damaged and could not be counted. Mean clutch size ($n = 10$) was 5.0 ± 1.4 SD, range: 3–8 eggs. Lemm (2006) in his field guide, reported 11 as the maximum clutch size for *G. copeii*, although we suspect Lemm's statement is in reference to *Gambelia wislizenii* (see Parker and Pianka 1976). Linear regression analysis indicated the positive correlation between female SVL and *G. copeii* clutch number was not significant ($P = 0.064$, $r^2 = 0.366$). This may reflect our small female sample size. The smallest reproductively active female (follicles > 5 mm) was from May and measured 83 mm SVL (CAS 57865). We noted the presence of one *G. copeii* female from March with corpora lutea from a previous clutch (SDSNH 26753), two other females from March with enlarged follicles (> 5 mm), and one female from June with oviductal eggs and concomitant yolk deposition for a subsequent egg clutch (MVZ 37260). These observations provide evidence that *G. copeii* may produce multiple annual clutches. In addition, the female in March with corpora lutea had sufficient

Table 2. Seasonal changes in the ovarian cycle of *Gambelia copeii*; * = oviductal eggs and concurrent yolk deposition for second clutch; ** one clutch was not counted.

Month	n	No yolk deposition	Early yolk deposition	Enlarged follicles > 5 mm	Oviductal eggs	Corpora lutea
March	4	0	0	3**	0	1
April	6	4	2	0	0	0
May	8	1	0	5	2	0
June	2	0	0	1**	1*	0
July	2	1	0	0	1**	0
October	1	1	0	0	0	0

time to produce a subsequent clutch, as did the other two March females with enlarged ovarian follicles. Fitch (1970) also reported two female *Gambelia sp.* from Baja California as being gravid in March. Our findings support Fitch (1970) and Lemm (2006), that two clutches may be produced by *G. copeii* in optimal years.

In view of the extensive geographic range of *G. copeii* (Grismer 2002), subsequent studies are needed to ascertain the degree of geographic variation in the reproduction of this species. Fitch (1985) reported clutch sizes of the congeneric *G. wislizenii* tended to be larger in the southern part of its range. Grismer (2002) observed a female with breeding coloration during late August near Todos Santos in the cape region of Baja California Sur. However, use of breeding coloration in museum specimens as an indicator of reproductive activity in natural populations, is not possible, as the pigments fade in alcohol.

Acknowledgments

We thank Jens Vindum (CAS), Christine Thacker (LACM), Carol Spencer (MVZ), and Brad Hollingsworth (SDSNH) for permission to examine specimens.

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Appendix I

Gambelia copeii examined from the California Academy of Sciences (CAS), Natural History Museum of Los Angeles County (LACM), Museum of Vertebrate Zoology (MVZ), and San Diego Society of Natural History (SDSNH). California, San Diego County: CAS 57865, SDSNH 46099, 55251; Baja California: CAS 11547, MVZ 31794, 50017, 50020, 140756, 140757, 161174, LACM: 4005, 4006, 4932, 15708, 126596, 126598, 137898, SDSNH 5078, 5079, 17470, 18118, 18945, 18946, 26752, 26753, 43007, 52959; Baja California Sur: CAS 56105, 65857, 90297, 90458, 147739, 147750, MVZ 13150, 13151, 37260, 37261, 37262, 50018.

Bull. Southern California Acad. Sci.
109(1), 2010, pp. 18–21
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Structural Irregularities in Sagittal Otoliths of Black Croaker (*Cheilotrema saturnum*) from Southern California

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Black croaker, *Cheilotrema saturnum*, is a sciaenid (Family Sciaenidae) common to the coastal nearshore ichthyofauna assemblage of southern California (Miller et al. 2008). Sciaenids, on average, are highly acoustic, both producing and receiving sonic vibrations via resonance through the swimbladder (Nelson 2006). Further acoustic sensing is facilitated by their relatively large sagittal otoliths, and extensive lateral line morphology (Nelson 2006; Helfman et al. 1997). Irregularities have been known to occur in sagittal otoliths, although this has historically been restricted to replacement of aragonite by vaterite as described in rockfishes (Love et al. 2002), salmon (Gauldie 1986, Sweeting et al. 2004), trout (Bowen et al. 1999, Melancon et al. 2005) and halibut (Tobin et al. 2005). During a characterization study of black croaker life history (Miller et al. 2008), irregularities were observed in a subset of sectioned otoliths. These irregularities often consisted of holes near the otolith core surrounded by discolored aragonite (personal observation). Additional sampling consistent with the methods described by Miller et al. (2008) was completed to investigate these irregularities.

A total of 805 samples were collected between 2001 and 2003 and stored in paper coin envelopes until later processing in the laboratory. The standard length (mm) and collection site were recorded for each individual, and the age was later determined by Miller et al. (2008). An additional 61 individuals were collected from Newport, California on 15 June 2004 using the same gill nets described by Miller et al. (2008). Sagittal otoliths from these individuals were preserved in 90% ethanol in the field and stored until processing in the laboratory. Each otolith was weighed to the nearest 0.0001 gram and heated in an oven at 200°C for 24 hrs, and reweighed. The percent weight loss was calculated after the otoliths were removed from the oven. Ten samples with percent weight losses ranging from 1.64% to 3.67% were sectioned using the same techniques used by Miller et al. (2008). The presence or absences of an irregularity in the section was recorded for each. An irregularity was classified as any depression on the face of the transverse section large enough to be seen under stereoscope magnification (Figure 1). Distribution of irregularities within the original 805 samples was examined by age class, mean standard length within each age class, and site of collection. The distribution of irregularities by site was ln(x) transformed to achieve a normal distribution. Percent weight loss and presence/absence of holes in otoliths from the 15 June 2004 collection and each distribution data set were statistically analyzed with a one-way analysis of variance (ANOVA; Sokal and Rohlf 1995).

Of the original 805 otoliths collected, 357 (44%) were observed with structural irregularities in the otolith (Figure 1). No significant differences were detected with

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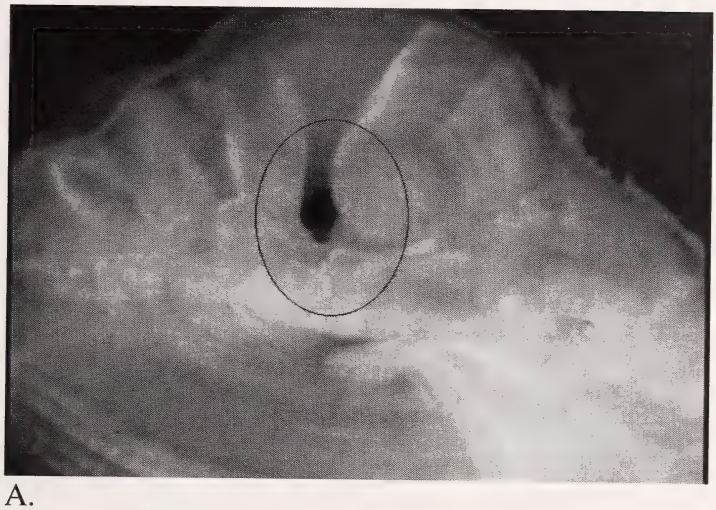
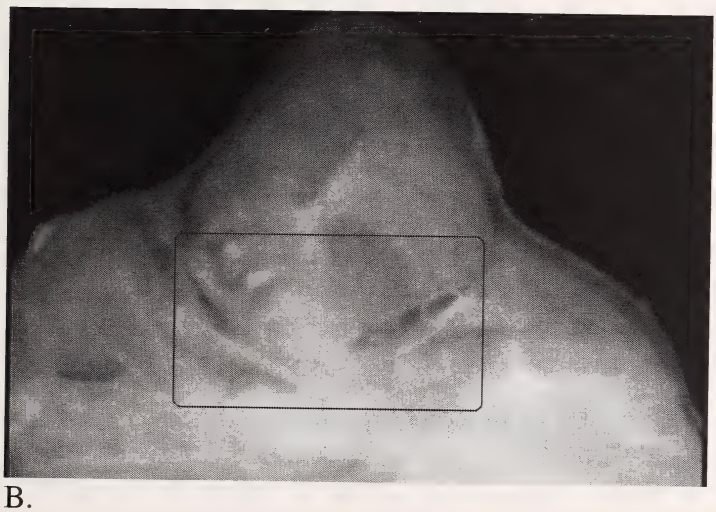


A.



B.

Fig. 1. Typical deformities observed in *Cheilotrema saturnum* sagittal otoliths, such as holes (A) and depressions (B) observed near the primordium on transverse sections of the otolith.

respect to age class (Figure 2; $F_{1,40} = 0.39$, $p = 0.54$), mean standard length in each age class ($F_{1,35} = 0.44$, $p = 0.51$), or collection site (Figure 2; $F_{1,14} = 0.29$, $p = 0.60$). Subsequent to heating, black croaker otoliths lost 2.54% of their mass, on average, ranging from 1.54% to 6.50%. In the 10 otolith subsample that was sectioned, deformities were significantly more common in sagittal otoliths that lost more than 2.5% of their mass after heating ($F_{1,8} = 34.43$, $p < 0.001$). The heating process applied to samples collected on 15 June 2004 accelerated the decomposition rate of organic material within the otolith, similar to what may have occurred while the otoliths were stored dry in paper envelopes without the addition of preservatives. The current investigation suggests that the appearance of irregularities in the section may be indicative of greater levels of organic material within the otolith, especially near the core. Such irregularities have not

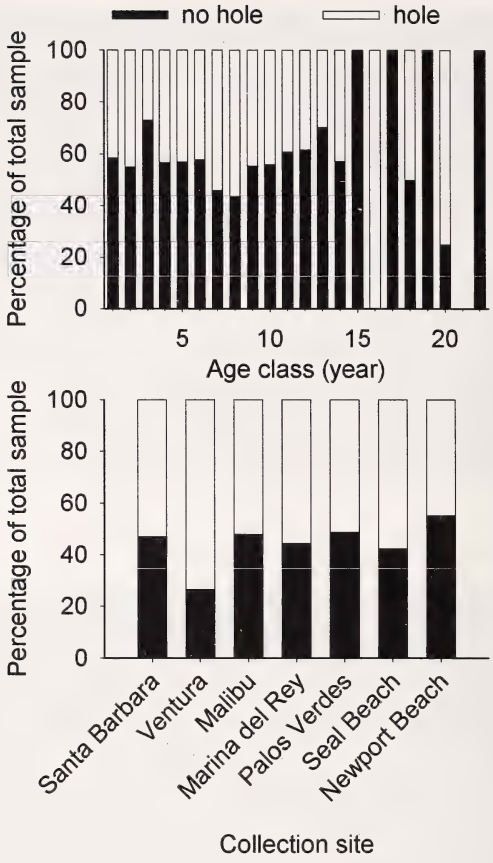


Fig. 2. Mean standard length of individuals with otolith irregularities and normal otoliths by age class and the distribution of occurrence of otolith irregularities as a percent of total observations by collection site in black croaker.

been observed in other sciaenids common to southern California, such as white croaker (*Genyonemus lineatus*; M. Love[2] personal communication), spotfin croaker (*Roncador stearnsii*; D. Pondella[3] personal communication), and California corbina (*Menticirrhus undulatus*; personal observation). Structural deformities, such as vaterite, have been observed in white seabass otoliths collected in southern California (J. Williams[4] personal communication), but such holes have not been described in sectioned white seabass otoliths.

These results suggest the irregularities observed in black croaker sagittal otoliths resulted from the decomposition of high organic content while awaiting processing. It is unknown what effect, if any, the high concentration of organic material has on the behavior of the individual. The occurrence of these irregularities in older size classes (Figure 2) indicates a lack of any deleterious impacts on the survivorship of black croaker. Furthermore, the absence of these irregularities in other members of the family

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[4] Jonathan Williams, Vantuna Research Group, Occidental College, Los Angeles, California.

common to southern California indicates the deposition of excess organic material in black croaker sagittal otoliths may be a species-specific anomaly.

Acknowledgments

This study was advanced through consultation with S. A. Bortone, G. M. Cailliet, M. P. Franklin, D. Kline, and M. S. Love. Collections were made in conjunction with the white seabass gillnet monitoring program, funded by the California Department of Fish and Game Ocean Resource Enhancement and Hatchery Program, facilitated by Steve Crooke. L. G. Allen and D. J. Pondella provided facilities and advice. D. J. Pondella and D. S. Beck commented on earlier drafts of this manuscript.

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